

CASTE AND REPRODUCTION IN ANTS: NOT ALL MATED EGG-LAYERS ARE "QUEENS"*

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The existence of two classes of adult females is characteristic of the *highly-eusocial* insects, which comprise termites, ants, various bees (*Bombus*, *Apis*, Meliponini) and vespine wasps. Queen and worker castes differ phenotypically as a result of morphological adaptations for efficient reproduction (dispersal, egg-laying) and maintenance activities respectively. Reproductive role partitioning in highly-eusocial species is specified by caste membership, but exceptions exist (for example, ponerine ants without queens). By contrast, in *primitively-eusocial* insects, adult females are all similar in form. Individual differences in size often occur as a result of environmental variations during larval growth (such as nutrition) and, together with age and insemination, are the basis for reproductive differentiation (reviewed by Wheeler 1986). Thus, although reproductive division of labor is a feature of both primitively- and highly-eusocial insects, it is achieved in two distinct ways: role differentiation among monomorphic adults, or production of alternative adult phenotypes. This dichotomy is not reflected by the current use of "queen," "worker" and "caste." Each of these terms has alternative meanings, and this, we suggest, obscures various evolutionary processes associated with eusociality.

The two meanings of caste

Dimorphic adult females are produced by divergent developmental pathways coordinated by endocrine signals, and this involves the expression of different sets of genes (see Wheeler 1986, Craig and Crozier 1978, West-Eberhard 1986). "Caste" has been used (as early as Latreille 1802) to distinguish these distinct female phenotypes. However, "caste" has also become a synonym for the separation of reproductive and sterile roles (e.g. Michener 1985: 303; Wilson 1985: 308; Fletcher and Ross 1985), or it sometimes serves to describe the

*Manuscript received by the editor July 12, 1988.

partitioning of non-reproductive activities among workers (e.g. brood care, foraging). In his major contribution (outlined in Wilson 1985) to the study of the ergonomic design of colony organization in ants, E. O. Wilson has adhered to a functional concept of caste: "a set of colony members . . . that specialize on particular tasks for prolonged periods of time." This definition stems from the need, for the purposes of optimization studies, to define age groups (= "temporal castes") as equivalent to morphological castes (Wilson 1968). Thus "caste," which originally denoted alternative female phenotypes, is now also used solely to describe role. This leads to ambiguity in the literature, because to some authors "caste differentiation" refers simply to reproductive division of labor, while to others it refers to morphological dimorphism. We suggest that it is useful to restrict "caste" to denote groups of female adults which have distinct phenotypes following pre-adult differentiation. This usage will give proper emphasis to the significance of morphological specialization, which is characteristic of the highly-eusocial insects. "Caste" should not be used to describe groups of workers whose behavior is age-correlated, or fertile as opposed to sterile females. Age-correlated behavior occurs throughout the animal world (Caro and Bateson 1986), and should not be equated with dimorphism in morphology.

A terminology based on form or function?

The equivocal use of "caste" is paralleled by that of "queen" and "worker". In highly-eusocial insects, "queen" denotes the existence of a developmentally-distinct reproductive caste with specialized morphological traits, except that in various bumblebees queen-worker dimorphism is limited to a set of physiological changes (Röseler 1977). In contrast, Michener (1974: 373), Fletcher and Ross (1985) and others use "queen" to describe role ("colony member that is primarily active in egg-laying and relatively or totally inactive in foraging"). The use of this operational criterion is common in primitively-eusocial bees and wasps, and thus authors studying different taxonomic groups differ in their use of "queen". This needs not be ambiguous to non-specialist readers provided that the absence of (phenotypic) castes is made explicit. We are concerned however that "queen" is also used in a functional sense in various highly-eusocial species in which secondary modifications have resulted in caste and reproductive role being no longer concurrent.

Workers also can reproduce

The queen caste has been lost in several ponerine ants, and mated workers lay all the eggs (Peeters 1987). Reproductive differentiation in queenless ants is analogous to that in primitively-eusocial wasps and bees since it occurs in the adult stage. A major difference however is that queenless ponerine colonies consist exclusively of members of the worker caste, while primitively-eusocial colonies consist of undifferentiated females.

Problems in terminology arise when describing individuals from the same morphological caste that perform different roles. Mated ponerine workers are the functional reproductives in a colony, but if they are designated as “queens” (e.g. Hölldobler and Bartz 1985) their developmental origin is disguised. They clearly differ from members of the queen caste, because they cannot start new colonies independently, and they have a lower egg-laying rate as a result of simpler ovaries (Peeters and Crewe 1985). Furthermore, in *Rhytidoponera confusa*, colonies can have either one queen or several gamergates, which is a major biological difference (Ward 1983). A description specifying both phenotype and role is thus sometimes necessary, for example “unmated workers laying diploid eggs” (in the myrmicine *Pristomyrmex pungens*; Itow et al. 1984), or “mated laying workers”. The latter have been termed “gamergates” partly for convenience, and partly to highlight this eusocial alternative and distinguish them from wingless queens with an external worker appearance (= ergatoid) (Peeters and Crewe 1985).

Buschinger's proposed nomenclature

Buschinger (1987 and earlier publications) also recognized that there is a need for a combination of structural and functional terms to describe the members of non-orthodox ant societies. Buschinger has suggested that “queen” and “worker” take on a strictly functional meaning (reproductive or not), and that new terms be adopted to describe morphology in all Hymenoptera. For example, mated egg-laying workers (“gamergates”) would be called “ergatomorphic queens”, and infertile queens would be “gynomorphic workers”. It is crucial to note that Buschinger (pers. comm.) understands these new terms to refer to *external* morphology only; this stems from the very precise meaning of the German word “Morphologie”. Since characters such as ovariole number or presence of

spermatheca are excluded, there is not always a precise correspondence between Buschinger's new terms and the phenotypes of adult females. A case in point might be a species with ergatoid queens where queen-worker dimorphism is most obvious with respect to internal differences such as reproductive organs. Buschinger's nomenclature has a clear taxonomic aim: visual appearance and role are combined in order to identify colony members. In contrast, we advocate that the terms "queen" and "worker" be used consistently in a structural sense across all highly-eusocial species, so as to gain an evolutionary perspective of the developmental origin of reproductive individuals. It is only in a minority of ant species that there will be a need for appropriate modifiers to describe roles (or appearance, e.g. "ergatoid").

Conclusions

"Queen", "worker", and "caste" are deeply embedded in the literature on eusociality, yet they are currently ambiguous. Reproductive division of labor, and the occurrence of (phenotypic) castes, are two completely distinct phenomena associated with eusociality—the former can occur without the latter. A more rigorous use of these terms, with the emphasis on morphology rather than on function, is likely to produce a better insight into various evolutionary modifications associated with eusocial organization, for example reproduction by mated workers in some ponerine ants. Wheeler (1986) emphasized that increased complexity of social organization has required changes in the underlying developmental programs that produce the members of a society. The evolutionary divergence of queen and worker morphology in some groups is thus fundamental, and this must be appreciated through a discriminating use of the terminology.

SUMMARY

The term "caste" has an equivocal meaning in writings on eusocial Hymenoptera. It is used in a morphological sense to describe the different female phenotypes which result from separate patterns of larval development, or it is used in a functional sense to describe reproductive role (or the individuals who perform that role). Similarly, "queen" and "worker" have alternative definitions. Various authors use "queen" to describe the phenotype which is a result of morphological adaptations for more efficient reproduction. Others

use “queen” simply to describe individuals which are mated and fertile. This confused practice obscures the fact that morphological castes do not exist in many eusocial hymenopterans. Thus, in *primitively-eusocial* species, reproductive division of labour occurs among morphologically-undifferentiated female adults. In contrast, in *highly-eusocial* species, female adults have one of two different phenotypes, and normally only members of the queen caste reproduce. However, in several ponerine ants, the queen caste has been lost, and some of the workers mate and lay eggs. The latter have sometimes been called “queens”, which conceals their developmental history.

We advocate that “caste”, “queen” and “worker” be used only in a strict morphological sense (including both internal and external characters), with an additional mention of role when this does not correspond with caste membership.

ACKNOWLEDGMENTS

We are grateful to B. Bennett, W. L. Brown, Jr., A. Buschinger, R. Crewe, M. Crosland, M. Elgar, M. Schwarz, M. J. West-Eberhard, D. Wheeler and E. O. Wilson for their comments and criticisms of various drafts of this manuscript, although not all of them agree with our views. We thank the Australian Research Grants Scheme for support to R. H. Crozier.

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